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Polycodium

C. B. ROBINSON

The statements by which Professor E. L. Greene* suggested the resuscitation of Rafinesque's name require quotation in full, as they bring up many points open to controversy.

"We have in the Eastern and Southern United States two groups of vacciniaceous shrubs either of which is at variance with all genuine *Vaccinium* in two important points of floral structure. The corollas in both groups are campanulate, while in both *Vaccinium* and *Gaylussacia* they are urceolate. The stamens also, in these campanulate-flowered shrubs, are of a structure so peculiar that, on the characters of this organ alone, a genus might reasonably be established, were concomitant characters wanting. *Vaccinium* and *Gaylussacia* are now everywhere admitted as distinct, yet, exclusive of the groups here under special notice, there is not the slightest difference of floral structure between the two. But these other shrubs depart widely from the characters of both *Vaccinium* and *Gaylussacia* not only in their open-campanulate corollas, but in respect to their stamens, which organs are doubly marked by extremely long and slender anther-tubes, and two prominent horn-like projections on the back; so that nothing approaching these characters is found in any other genera allied to *Vaccinium*.

"Twice in the early part of the century, botanists of first-class ability proposed the separation of these species from *Vaccinium*. Rafinesque in 1818, not distinguishing generic differences between those types represented by *V. stamineum* and *V. arboreum* respectively—perhaps not even knowing *V. arboreum*—proposed the *V. stamineum* group for a genus under the beautifully appropriate name of POLYCODIUM; and Nuttall in 1843, ignoring Rafinesque's earlier proposition—just as later pretenders to taxonomic autocracy suppressed Nuttall's work—sought to establish a new genus *Batodendron* with *V. arboreum* as typical, and *Picrococcus* with *V. stamineum* for its type.

"The characters of the two genera are well indicated by Nuttall, in the transactions of the American Philosophical Society, with the exception of one new and most significant peculiarity of the *V. stamineum* group which I alone seem to have observed.

* Pittonia 3: 323. 1898.

It is this, that in this group the corollas are *open in the bud!* For from ten days to two weeks before the actual flowering, and even from the time that the buds are green and scarcely larger than a pin-head, the corolla is open and campanulate. This is another character otherwise unknown in the family of plants to which these belong. Certainly in *Vaccinium* and *Gaylussacia* the buds are tightly closed, in an imbricate aestivation, until the corollas are full-grown and the anthers mature."

Now of vacciniaceous plants found within the limits of the United States, the genera that are almost universally recognized are *Chiogenes*, *Gaylussacia*, and *Vaccinium*. Even regarding these there is some controversy. *Chiogenes* is readily distinguished by the position of the ovary, only slightly inferior in flower, distinctly inferior in fruit, and while American and British authors of recent years have agreed in placing it near *Vaccinium*, German authors on the other hand believe the closest affinity to be *Gaultheria*; and it can hardly be denied that its position is somewhat intermediate,

There is no doubt as to the identity of *Gaylussacia*, as it was published as monotypic, its type, *G. buxifolia* H. B. K., agreeing with many species now known from South America, in the possession of evergreen leaves and non-succulent fruit as well as of a 10-celled ovary. The only species described as a *Gaylussacia* from Mexico or Central America does not belong to the genus, all of the species so called in the United States have succulent fruit, and all but one have deciduous leaves. Niedenzu* has placed that one in the *Vitis-Idaea* section of *Vaccinium*, and the other North American species in the *Cyanococcus* section of *Vaccinium*, retaining the name *Gaylussacia* for South American species only.

Kuntze,† also, has taken up the name *Adnaria* Raf.‡ for *Gaylussacia*, but the most positive thing that can be said about Robin's description,§ upon which Rafinesque's was based, is that it does not agree with that of any species of the family found in America and in particular disagrees with *Gaylussacia* in the very character relied on for its differentiation, the number of cells in the ovary.

* Engl. Bot. Jahrb. 11: 193. 1889.

† Rev. Gen. Pl. 382. 1891.

‡ Fl. Ludov. 56. 1817.

§ Voy. Int. Louisiana 3: 422. 1807.

Yet, taken on a summary of characters, there is probably no species found in Louisiana that is more likely to have been the basis for Robin's description than *Gaylussacia dumosa* (Andr.) A. Gray.

All of the remaining species of the family found north of the Mexican border are retained by many authors in *Vaccinium*. Generic or sectional segregation has been proposed on several characters, taken singly or in combination, the degree of union of the corolla, its aestivation, its shape, the presence or absence of awns on the anthers, the presence or absence of pubescence on the filaments, the presence or absence of false partitions in the ovary, the nature of the inflorescence, and tetramerous as contrasted with pentamerous flowers.

In the Thibaudieae, the other subfamily of Vacciniaceae, general agreement has been reached that the primary basis of differentiation should be sought in the stamens. There is much reason to believe that this is equally true with regard to the *Vaccinium* group, but it would be useless to belittle the fact that the weight of botanical opinion has been otherwise. The most popular segregate has been *Oxycoccus*, from which *Hugeria* has further been discriminated. They differ from the remainder of the group and from one another in the degree of division of the corolla. Possibly *Polycodium* will prove the most acceptable of the others. But on what grounds should it be retained? Professor Greene's claims for it are excessive, although indefinite, for he does not define "genuine *Vaccinium*." It has a campanulate corolla: so have *V. arboreum* Marsh.,* *V. Vitis-Idaea* L., *V. poasanum* Donn. Sm., *V. confertum* H. B. K., and others, differing from one another in various characters, and none except the first closely allied to *Polycodium*. The 10 stamens of *Polycodium* have pubescent filaments and 2-awned anthers: except in number they differ from the great majority of species of the eastern and southern United States, which have pubescent filaments but awnless anthers (section *Cyanococcus*), from most of those of the western States, which have 2-awned anthers but glabrous filaments (section *Euvaccinium*), but agree with many tropical American species,

* No opinion is necessarily expressed in giving the name of this or any other species as *Vaccinium*.

such as *V. leucanthum* Schlecht., *V. stenophyllum* Steud., and *V. cubense* Griseb., none at all closely allied to *Polycodium*. This is not all, for in the United States no single character is as certain to ensure the instant identification of *Polycodium* as the long-exserted anthers; moreover, the tubes forming the prolongation of the anther cells are unusually long, both absolutely and relatively to the anther cells. But there is a Mexican species, *Vaccinium Kunthianum* Klotzsch, so closely related to *Polycodium stamineum* that neither Kunth nor Dunal* thought it worthy of specific rank. Its stamens were described as half-exserted, and figured as well exserted, but in no collection that I have seen, so identified by others or by myself, can they be considered as more than barely exserted, the anthers are shorter than in the other species, and the anther tubes only about one and a half times the length of the anther cells. In all other respects it is a perfectly good *Polycodium*, and if the genus is to be maintained, must be transferred to it, forming a section by itself, on the basis of the characters just stated.

Finally, the anther awns are often revolute, but too much emphasis should not be placed on this, as it is not always constant within a single flower; at least, however, they are divaricate, but so they are in species which no one has suggested separating from *Vaccinium*, such as *V. caespitosum* Michx.

The flowers of *Polycodium* are articulated with the pedicel; this is also true of certain species placed in *Vaccinium* by most authors, notably of the *Disterigma* species. That group, which does not come north of Mexico, was until recently treated by all authors as a section of *Vaccinium*, but Niedenzu† and Hörold‡ so far separate it from that genus that they place it in the Thibaudieae. On the basis of floral characters there seems to be no reason for so wide separation; indeed, unless *Vaccinium* is to be radically divided, I at least believe that there is as much reason for placing *V. Myrtilus* L. and its American allies in a different genus from *V. corymbosum* L. and its allies, as there is for so segregating *Disterigma* from the latter. Drude§ has placed considerable

* H. B. K. Nov. Gen. & Sp. 3: 267. pl. 253. 1819; DC. Prodr. 7: 568. 1839.

† Engl. Bot. Jahrb. 11: 209. 1889.

‡ Engl. Bot. Jahrb. 42: 282. 1909.

§ Engler & Prantl, Die Nat. Pflanzenfam. 4¹: 32. 1889.

emphasis on articulated pedicels as a means of distinguishing the Thibaudieae from the Vaccinieae but, unfortunately, has gone far beyond the facts.

One character remains to which Professor Greene has called particular attention, the open aestivation of the corolla. All evidence that has been obtained confirms his statement on this point for every species of *Polycodium*, including *V. Kunthianum*. This does seem of such importance that the genus may properly be maintained; the other characters previously mentioned may be treated as collateral, by one who is dealing with the species of America north of Mexico, but it must be remembered that not one of them can be relied on to distinguish *Polycodium* from all other genera, even within the limits of North America.

Rafinesque* published *Polycodium* thus: "67. The species of *Vaccinium* with campanulated corollas, must form a peculiar genus or subgenus, *Polycodium*. In fact the whole tribe of *Ericacea* or *Bicornia* must be newly modelled." And this is all, with one very important exception. The paragraph occurs in a review of Pursh's *Flora Americae Septentrionalis* and may fairly be interpreted by reference to that work. Pursh divided *Vaccinium*† primarily into species with deciduous leaves and those with evergreen leaves, dividing each of these in turn on the basis of campanulate as contrasted with urceolate corollas. His species with deciduous leaves and campanulate corollas were *V. stamineum*, *V. album*, *V. arboreum*, *V. dumosum*, *V. frondosum*, and *V. pallidum*; those with persistent leaves and campanulate corollas were *V. Vitis-Idaea*, *V. myrtifolium*, and *V. crassifolium*. *Vaccinium stamineum* thus comes first, and *V. album* Pursh is regarded by most authors as the same species. *Polycodium*, therefore, may be held to be typified by *Vaccinium stamineum* L., but Rafinesque's genus in its entirety was a mixture of widely differing elements, including representatives not only of *Batodendron* but of *Gaylussacia* and of different sections still included in *Vaccinium* by nearly all authors.

Picrococcus of Nuttall is based almost entirely on *Vaccinium stamineum* L. (including *V. elevatum* Banks & Soland.) with the

* Am. Monthly Mag. 2: 266. 1818.

† Fl. Am. Sept. 1: 284-290. 1814.

addition of a second species, *Picrococcus floridanus*, certainly congeneric with the former, of which more hereafter.

Professor Greene is unduly critical of Nuttall for overlooking or disregarding such a publication as Rafinesque's of *Polycodium* for the genus containing *Vaccinium stamineum*, and Nuttall was not the first offender. In 1836 Rafinesque himself has the following:* "ADNARIA Raf. fl. lud. probably a subgenus of the *Codorolla* or *Vacciniums* with bell flowers, which see." But *Codorolla* does not appear again, and Rafinesque did not consider this reference worth indexing.

It is apparent that the adoption of *Polycodium* as a generic name, to be typified by *Vaccinium stamineum* L., is barely justified.

Before leaving the subject of generic subdivision in the *Vaccinium* alliance it is desired to amplify a statement above made with regard to the importance of characters derived from the stamens. The anthers may be 2-awned or awnless. In a solitary specimen, *Wright 2202*, referred to *Vaccinium Ramonii* Griseb., some anthers were found with a single central awn. Further examination showed that this was not a constant character, even within a single flower; but none of the anthers were awnless. The value of anther awns as a diagnostic character obviously depends upon the degree of their constancy, and final judgment will be influenced, consciously or unconsciously, by the nature of the grouping thus achieved.

Examination of the flowers of every species but one, found within the limits of North America, as well as of some extralimital material, gives this result. There are 3, or more likely only 2, species, *V. meridionale* Sw., of Jamaica, *V. consanguineum* Klotzsch, of Panama and Costa Rica, and *V. multiflorum* Benth., of Colombia, in which this character has to be handled with extreme caution. All of these are very closely allied; indeed, it is doubtful if the first two can be held distinct. In all of these the awns are very delicate and often closely appressed, to such an extent that they might escape detection, unless considerable care be taken in their search. Further, in *V. meridionale* they are often so reduced that they are practically wanting, yet other stamens in the same flower may possess them, slender and short

* New Fl. 1: 65. 1836.

indeed, but certainly present. Moreover, *V. multiflorum* was described as having anthers alternately awned and awnless, yet a recent collection from near its type locality, *Pittier 1182*, agreeing otherwise with Bentham's description, has all the anthers of such flowers as were examined 2-awned, with awns as described and found for this and for *V. consanguineum*. The plate* of *V. meridionale* is wrong in this respect.

Yet, all these can be described as awned anthers, and on other grounds the alliance of the species is with those possessing awned anthers. Much search has failed to disclose a single other exception, not only within the limits of a species but within the limits of what appear to be groups of related species.

It may be added that the presence of pubescence, in whatever degree, on the filaments or the connectives—and when it occurs it is usually on both—is equally conclusive but of secondary importance. Thus, if a vacciniaceous plant be found in America north of Mexico with awnless anthers and glabrous filaments, no further information is needed for its determination as *Gaylussacia frondosa* (L.) T. & G., except by those who consider *G. nana* (A. Gray) Small and *G. tomentosa* (Pursh) Chapm. to be specifically distinct from that species. Each of the other three combinations of these two characters will describe large groups of species.

On the other hand, investigation of the relative length and degree of divergence of the awns and of the relative amount of pubescence on the filaments seems to indicate that these do not afford reliable characters except possibly in rare cases.

Up to the present the following have been ascribed to *Polycodium* as distinct species: *P. caesium* Greene, *P. candicans* (C. Mohr) Small, *P. elevatum* (Banks) Greene, *P. floridanum* (Nutt.) Greene, *P. Langloisii* Greene, *P. melanocarpum* (C. Mohr) Small, *P. neglectum* Small, *P. oblongum* Greene, *P. oliganthum* Greene, *P. revolutum* Greene, and *P. stamineum* (L.) Greene; it has already been stated that another species awaits transfer, *Vaccinium Kunthianum* Klotzsch. The last having been separated on the basis of its shorter anthers, not or barely exerted, the character depended on as of next importance is the relation between leaves or bracts and the inflorescence.

* Sw. Ic. Ind. Occ. *pl.* 12. 1794.

In the *Vaccinium* group as a whole there is a transition in this respect, and *Polycodium* is merely one case of many. In certain species, such as *V. caespitosum* Michx., *V. scoparium* Rydb., and *V. Myrtillus* L., the flowers are few in number on a branch borne in the axils of what are apparently quite normal leaves as to size, shape, and texture. In others the inflorescence is quite clearly racemose, or by contraction fasciculate, the pedicels subtended by bracteoles quite different in appearance from the vegetative leaves. This includes nearly all the species of the eastern United States. There is yet a third group, which almost perfectly links the two, the inflorescence being perhaps best described as a leafy raceme. These are mostly tropical plants. Incidentally, these three groups follow rather closely the lines indicated by the stamens.

In the case of *Polycodium* there is a group "in which," to use Nuttall's expression* when describing *Picrococcus floridanus*, "the flowers appear truly axillar." Here also belong the names *Polycodium caesium* Greene, *P. oliganthum* Greene, and *P. revolutum* Greene. Nuttall's type seems to have perished, which will cause trouble to those who believe this group to contain more than one species, for he has no sufficient description for more definite determination. In the case of the other species duplicates of the type collections have been examined, and there seems no sufficient reason for holding them distinct. In separating *P. revolutum* from *P. caesium* Professor Greene† relies chiefly on the leaves of the former being more pubescent, more oval and obtuse, their margins revolute, the calyx lobes deeper, acute or acuminate instead of scarcely acute, and deeper corolla lobes. It is not possible to separate the series of specimens on these characters or any of them, those drawn from the leaves being especially unreliable, not even holding for the collections on which the species were based. There seems even less reason for segregating *P. oliganthum*.

Now, the same thing happens in *Polycodium* as in the *Vaccinium* group in general; the leaves, in the axils of which the flowers are borne, are often reduced in size but still retain the other characters of the typical leaves of the plant; yet again, they may

* Trans. Am. Philos. Soc. II. 8: 262. 1843.

† Pittonia 3: 249, 250. 1897.

be very greatly reduced although sometimes differing considerably within the same inflorescence. *P. oliganthum* approaches the former condition but seems to have been referred correctly to the *P. floridanum* group. The linking material affords some justification for the view that specific lines should not be drawn on this character, but the corolla in the group thus separated is always smaller, one half to one third of the length of that of the remaining species, and it seems preferable to consider it as distinct and as forming a single species only. Its range is from South Carolina to Florida, all of the types of the species proposed having come from the latter state. If this view be accepted, there seems no reason why its name should not be *Polycodium floridanum* (Nutt.) Greene.

From the remainder it is exceedingly easy to separate *Polycodium neglectum* Small by means of its glabrous branchlets and leaves. These characters hold definitely for large series of collections, but there seem no others correlated with them, and the plants often grow side by side with those of *P. stamineum*. It is, therefore, a matter of opinion as to whether the two should be held distinct.

Polycodium melanocarpum was described by Mohr* as *Vaccinium stamineum melanocarpum* without a definite type specified. It was raised to specific rank by Kearney,† who expressly stated that his own collections were not typical. Mohr,‡ subsequently discussing it as a species, gives as the type locality "Mountain region of Alabama. More specifically, St. Clair County, near Ashville, July 1880." The ground for separation was the succulent nature of the fruit and its color. Mohr also proposed two varieties, *V. melanocarpum candicans* and *V. melanocarpum sericeum*. In Small's Flora§ the former variety becomes *P. candicans* (C. Mohr) Small, and *Polycodium melanocarpum* includes both the species and its variety *sericeum*; "hypanthium usually more or less pubescent." The seventh edition of Gray's Manual goes further: "calyx white-tomentose." Study of material in the herbarium of

* Bull. Torrey Club 24: 25. 1897.

† Bull. Torrey Club 24: 570. 1897.

‡ Contr. U. S. Nat. Herb. 6: 658. 1901.

§ Fl. SE. U. S. 894. 1903.

the New York Botanical Garden led to the conviction that *Vaccinium melanocarpum* of Gray's Manual is a good species, but that it is not identical with Mohr's species but with his variety *sericeum* only. On all sheets in the New York herbarium the character of pubescence on the hypanthium, always more or less definitely present on fruit as well, was accompanied by another character. The calyx lobes were accrescent in late flower or early fruit. This was easily evident to the eye, but on measuring, the balance of difference proved slight, the fruiting calyx being 1.5–2 mm. long in *P. stamineum* and 2.5–3 mm. long in the collections referable to *sericeum*. There was a single plant in which a glabrous hypanthium was accompanied by an accrescent calyx. This plant, on fine division, would be referred to *P. candicans* Small.

Examination of material from the United States National Herbarium shows that the same is true of the collections there. But the specimen that Mohr seems to have considered as the type of his species has a glabrous hypanthium, and the calyx is not accrescent. So far, then, as *Polycodium melanocarpum* (C. Mohr) Small is concerned, there is room for difference of opinion; if the character of succulent fruit is considered sufficient, it may be maintained as a species, but no other sufficient reason has been found for holding it specifically distinct from *P. stamineum*. But the evidence is otherwise as regards *V. melanocarpum sericeum*.

Typical forms of *P. candicans* (C. Mohr) Small differ notably from more typical *P. stamineum* in glaucescence, but the extremes are united by many intermediates, and no sharp line for separation has been found. Moreover, there is much reason for believing that this is a revival of *P. elevatum* Greene, the *Vaccinium album* of Pursh, although not the Linnaean species of the latter name, which does not belong to the family.

Two species have not been discussed, *P. oblongum* Greene and *P. Langloisii* Greene, of neither of which I have seen the types. Its author places the former in the *P. floridanum* group, but from the description and study of material which seems to match it I am inclined to refer it to *P. stamineum*, to which also *P. Langloisii* seems too closely related.

The following new combinations give effect to conclusions already stated.

Polycodium Kunthianum (Klotzsch) comb. nov.

Vaccinium stamineum β H. B. K. Nov. Gen. & Sp. **3**: 267. 1819.

Vaccinium elevatum β Dunal, in DC. Prodr. **7**: 568. 1839.

Picrococcus elevatus β Nutt. Trans. Am. Philos. Soc. II. **8**: 262.
1843.

Vaccinium Kunthianum Klotzsch, Linnaea **24**: 56. 1851.

Polycodium sericeum (C. Mohr) comb. nov.

Vaccinium melanocarpum sericeum C. Mohr, Contr. U. S. Nat.
Herb. **6**: 658. 1901.

Vaccinium melanocarpum Robinson & Fernald, in Gray, Man. ed.
7. 639. 1908. Not *V. melanocarpum* C. Mohr, 1897.

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